Escape Response of an Infaunal Clam *Ensis directus* Conrad 1843, to a Predatory Snail, *Polinices duplicatus* Say 1822.

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INTRODUCTION

Behavior that increases the risk of predation is usually attributed to infection by a parasite, which thereby increases its chances of moving to the next host. Curio (1976) reviews several cases of increased prey visibility, including a peculiar crawling behavior by an infaunal marine bivalve, *Macoma balthica* Linnaeus, 1758, infected by trematodes (Swennen, 1969). In this note I report a behavior that increased the visibility of an infaunal bivalve to gull predators, but which was not due to infection by a parasite. I show that this behavior is an avoidance response to a tactile predator, the moon snail, *Polinices duplicatus* Say, 1822. The palaentological implications of this interaction were pointed out to me by J. Levinton.

LOCATION & STUDY SITE

The study was carried out on the intertidal flats at Plymouth, a coastal lagoon 80km south of Boston, Massachusetts. Observations were made from 1975 through 1979. Experimental studies were carried out on White Flat (41°79'N, 70°40'W) during 1979. This flat grades from silty sand on its western (shoreward) side to fine well-sorted sand on its eastern side. An area of one kilometer by one-half kilometer is exposed twice a day for two to three hours. Razor clams ranging in size from 1 to 15cm in length were found on this flat in five successive years. Two naticids inhabited this flat: *Polinices duplicatus* and *P. heros* Say, 1822. The preferred prey of *P. duplicatus* has been described by Edwards (1975), while Wiltse (1978) has described the impact of this predator on prey numbers at a nearby lagoon, Barnstable.

RESULTS

The experiments grew out of a series of observations made throughout the lagoon over a 5 year period. Razor clams (*Ensis directus*) are active burrowers that normally dig rapidly into the sand when disturbed. Despite this, some clams were observed flipping themselves vigorously over the surface of the sand at low tide. This increased their risk of predation by gulls (*Larus delawarensis* Ord, 1815). Gulls were frequently observed feeding on razor clams, but never observed pulling a clam from the sand, or pecking at the sand to find prey. Clams dig rapidly into the sand after short excursions. The brief exposure was not consistent with the hypothesis of behavior modified by a parasite. Two clams found flipping over the flats were dissected. Both were free of trematodes.

The behavior occured at night, when clams could be located by the squirting sounds made as the clams flipped over the sand. Thus the behavior was not a response to deteriorating environmental conditions caused by heating of the sand during daytime low tides.

A chance observation suggested an alternative hypothesis. Some razor clams were observed with the siphon end protruding well out of the sand. In every case the foot of the clam, beneath the surface of the sand, was held by a predator; either a naticid snail (*Polinices duplicatus*) or a nemertean (*Cerebratulus lacteus* Leidy, 1851). This observation suggested that razor clams leave the sand to escape attack by these relatively slow moving predators.

To test the response of razor clams to naticids I pushed a clam part way into the sand directly in the path of a crawling naticid. As soon as the leading edge of the snail's foot touched the clam it dug rapidly into the sand. The snail dug rapidly down the hole left by the clam. After a minute or two the clam emerged foot first from the sand, within a meter or two of the point where it started. The slightly curved shell of the clam evidently contributed to the re-emergence. Upon emergence the clam twisted its foot back toward the siphon end, pushing down onto the sand with the foot until the shell rose enough out of the sand to topple over. The clam then propelled itself over the sand by a series of vigorous lashes with the foot, combined with rapid ejections of water along the ventral side of the foot.

I repeated the experiment with 10 clams collected nearby. In 5 cases the clams emerged from the sand at a distance from the point of attack, and flipped away. Clams that emerged in areas without standing water traveled less than a half meter before digging into the sand. Clams that emerged in puddles of standing water would propel themselves several meters through the water before digging back into the sand. In 3 cases the clam never re-appeared, and the snail soon re-appeared without the clam. In the remaining cases the clam emerged from the sand siphon first. Digging away the sand revealed the naticid grasping the clam and working its way downward toward the foot of the clam. The snail attacked the foot, leaving no hole in the clam shell to mark its attack.

I repeated the experiments with two common molluscs that co-occur with naticids on White flat. The gastropod *Nassarius trivittatus* Say, 1822 responded by rapid crawling or by flipping across the sand by vigorous contortions of the foot. *Tellina agilis* (Stimpson, 1857) did not always respond—some individuals flipped themselves by vigorous twists of the foot.

The experiment was repeated by collecting two species of snails from a nearby muddy flat, which was not inhabited by naticids. In each trial I placed a new snail in the path of an oncoming naticid, as in previous experiments. I repeated the experiment with five periwinkles (*Littorina littorea* (Linnaeus, 1758) and five mud snails (*Ilyanassa* [*Nassarius*] *obsoleta* Say, 1822) using 10 different naticids. None of the snails showed an escape response in response to touch by the naticid. The naticids did not complete their attack and eventually crawled away.

DISCUSSION

Escape responses result from direct contact with a predator, while avoidance responses are made at a distance, often through chemical cues (Phillips, 1977). Escape responses have been reported most frequently in gastropods (Gore, 1966; Kohn, 1961), but have also been found in scallops and an anemone (Yentsch & Pierce, 1955). Generalizations about the occurence of escape responses have not been forthcoming, although Mackie (1972) suggested that saponins were responsible for escape responses to asteroids. The reported cases of escape response by molluscs have all been to tactile predators (asteroids, gastropods), rather than visual predators (birds, crabs, etc). Escape responses vary in their occurrence among species within a habitat, and their specificity relative to any given predator (Mackie, *op. cit.*). At Plymouth, escape responses were not found in two common gastropods that do not occupy the same habitat as naticids. This degree of specificity suggests that escape responses are a co-evolved interaction between a predator and its prey. It would be interesting to examine the role of inheritance and learning in the maintenance of escape responses.

The fact that naticids grasped the clam beneath the substrate, with the siphon pointing upward, has some implications for interpreting the fossil record. Naticids left no trace of their attack on razor clams because they attacked the foot rather than drilling through the shell. A bed of razor clams would remain in life position after attack by naticids, and would appear to have been killed by burial.

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